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INHERITANCE OF PLUMAGE COLOR IN CROSSES OF BUFF AND COLUMBIAN FOWLS

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As a part of a search for material suitable for use in measuring the linkage strength of several sex-linked characters in poultry, some preliminary experiments have been undertaken on the inheritance of the Columbian plumage pattern. The results of these experiments have confirmed those of Sturtevant (1912) in establishing the sex-linked nature of one of the genes involved in the production of this pattern, and have demonstrated the relationship between it and the buff plumage coloration. The inheritance and somatic effects of the chief factor involved appear to be clear enough to make it useful in genetic investigations on poultry. A short description of the experimental results is therefore given here, to be followed by a more detailed report when further evidence is at hand.

The Columbian pattern, sometimes known as the Ermine coloration, is characteristic of several standard varieties of a number of breeds of poultry of which the Light Brahma, the Columbian Plymouth Rock and the Columbian Wyandotte are perhaps the most familiar. Although subject to some variation the pattern consists in general of a pure white surface color in all parts of the plumage except in the hackles, wings, and tail feathers, in which black is present either as a central stripe (hackles); as a solid color covering somewhat more than half the feather (primaries) or as a solid color covering the whole feather (tail). In typical Columbian fowls the undercolor or fluff at the base of the body feathers is generally lead or slate, which is sometimes so pronounced as to show through at the surface especially on the back.

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[1] Contributions in *Poultry Genetics*, Storrs Agr. Exp. Station.

This pattern is alike in both sexes except for the slightly different appearance caused by structural differences in the hackle and saddle feathers.

The down color of newly hatched Columbian chicks is white or a yellowish white like the down characteristic of the chicks of many white varieties of poultry, *e.g.*, White Leghorns. Black or gray markings appear on most Columbian chicks as a spot on the head, or as dorsal stripes on the head or back and in the developing wing quills. This pattern varies in different individuals from an entire absence of dark pigment to the presence of rather heavy dark dorsal stripes.

The color variety chosen for crossing with Columbian was buff, since this offered a clear contrast in the absence of white and the uniformity of coloration and because the plumage color of both sexes is practically the same. Moreover, buff is known to be recessive to many other plumage colors and patterns and for this reason is less likely to carry other factors which might complicate the results.

The first crosses were made between a Columbian male extracted from the second generation of a cross between Light Brahma and White Leghorn,[2] and purebred Buff Orpington females.

Twenty-three chicks were hatched from these crosses. Of these, twelve were predominantly white in the down, and eleven were buff. Of the whites four were pure white, five had a black streak or spot on the head and saddle, and black pin feathers appearing in the wings, and closely resembled purebred Light Brahma chicks in color; one was smoky white and two were white with a buff spot or streak on the head and neck. Of the buffs eight were clear buff in color, one was a very light buff and two were buff with black down on heads and saddles and with black feathers in the wings. All of the white chicks developed adult plumage resembling the Columbian pattern except that the black in the hackles, tail and wings was a dingy gray, occurring as stippling on the white ground rather than as a solid color. The buff chicks which survived developed adult plumage in which the hackles, tail and wing feathers were gray or black, while the feathers over the rest of the body were buff. These resembled mosaics of buff and Columbian in which the Columbian pattern was imposed on a buff ground.[3]

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[2] The cross of Light Brahma by White Leghorn (quoted by permission from unpublished data of Sinnott and Warner) when made reciprocally produced white birds in F_1, generally with some ticking with black and occasional brassiness or tinging with buff. The White Leghorns used were apparently pure for the dominant inhibitor of color (I) while the Light Brahmas contained the recessive allelomorph of this gene (i).

In tabular form the results of this cross were as follows:

TABLE I

Columbian Male × Buff Female

	White		Buff	
Down Colors	12		11	
	♂	♀	♂	♀
Adult Colors	6	6	3	6

The appearance of two kinds of offspring in equal numbers from this cross indicated that one parent was probably heterozygous in a factor causing the difference between white and buff. Later work showed this to be the male. When a *purebred* Light Brahma male was mated to purebred buff females (Orpingtons and Plymouth Rocks) the thirty-seven offspring were without exception white in the down and developed into white Columbians as adults. The dominance of white over buff was practically complete although one or two buff feathers were noted on one hybrid and a slight buff tinge on another.

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[3] The resemblance of these hybrids to descriptions and illustrations of early buff varieties (Tegetmeier, 1872) is quite striking. At present the only buff variety characterized by a considerable amount of black in hackles, wings and tail is the Buff Brahma, although this is not yet recognized by poultrymen as a standard type.

The coloration characteristic of the Rhode Island Red breed is essentially an ermine or Columbian pattern with a red ground substituted for the white of true Columbians. A very useful discussion of the relationships between these patterns from the standpoint of a breeder and fancier of long experience is given by Robinson (1921) see esp. pp. 55 and 56.

The offspring of the purebred Light Brahma male by buff females were much whiter than the chicks from the first male. Only one of the thirty-seven showed the dark head spot characteristic of Light Brahma chicks and all were of a clear dead white, lacking even the yellowish tinge characteristic of most white chicks in the down. As adults these birds were very similar to the first lot. The amount of black in hackles, tails and wings was about intermediate between the amount present in the Columbian parent and the absence of black in pure white birds.

The first generation hybrid chicks were crossed in two ways. The F_1 Columbian females were backcrossed to a purebred Buff Plymouth Rock male; the F_1 buffs were bred *inter-se*. The results of these matings are presented in Tables II and III.

TABLE II

Result of Crossing F_1 Columbian Females with Pure Buff Male.

	White		Buff		Total
Down Colors	36		38		74
	Columbian		Buff		
	♂	♀	♂	♀	
Adult Colors	14	0	0	21	35[4]

TABLE III

Result of Crossing F_1 Buffs inter-se

	Buff and White		Buff		Total
Down Colors	9		74		83
	Columbian		Buff		
	♂	♀	♂	♀	
Adult Colors	0	0	17	15	35[4]

From the backcross of F_1 Columbian females with a buff male equal numbers of buff and white chicks resulted, a clear monohybrid segregation. Evidently one factor determines the difference between white and buff, and from the F_1 results it is clear that white is the dominant allelomorph. This factor is however sex-linked, since all sons of the F_1 Columbian females are white (Columbian) while all the daughters are buff.

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[4] The differences between the numbers of chicks and the numbers of adults indicate the number of birds which died before definitive plumage or secondary sex characters were developed.

The mating of F_1 buffs *inter-se* produced only buff chicks, indicating that buff is recessive and breeds true. The nine chicks recorded as buff and white all had buff heads or wings or both and those which lived developed buff adult plumage. Genetically they were probably extremely light buffs.

As regards only the difference between white and buff, we may conclude that the Columbians contain a dominant sex-linked gene for the inhibition or restriction of buff from the plumage. The first male was evidently heterozygous for this factor; the second male was homozygous for it; the Columbian females contained but one dose of it, and this was located in the single sex chromosome; while all the buffs lacked it entirely. This is evidently the same gene (I) which Sturtevant (1912) found in Columbian Wyandottes, although its effects were somewhat obscured by other factors in his crosses with Brown Leghorn.

The presence of this gene in some White Wyandottes which I have studied strengthens the homology between the gene with which Sturtevant was dealing and the gene which is present in the Light Brahmas used in these experiments. I have recently crossed two White Wyandotte males with purebred Buff (Orpington) females. The white males were known to be recessive white (cc), *i.e.*, they lacked the gene (C) for the development of color in the plumage. The results of this cross are shown in the table following.

RESULT OF CROSSING WHITE WYANDOTTE MALES WITH BUFF ORPINGTON FEMALES

	White			Buff		Total
Down Colors	13			13		26
	Columbian			Buff		
	♂	♀	?	♂	♀	
Adult Colors	3	2	1	3	7	16

In addition to the types noted above three unclassified chicks were born from one mating. These were chiefly white in the down with black spots on the crown and neck and black quills in the wings. They resembled very dark Columbian chicks. These developed adult plumage different from the other chicks in this cross and could not be classified either as Columbians or buffs. Additional factors which have not been identified were probably contributed by one of the White Wyandotte males and further reference to these birds will therefore be postponed until more information is obtained. Omitting these, the salient fact concerning this cross is the production of only two classes of chicks, white (Columbian) and buff in equal numbers. The White Wyandotte males bred, therefore, like F_1 hybrids between Columbian and buff and were undoubtedly heterozygous in the gene for the restriction of buff. As adults the offspring of this cross were indistinguishable in color from the offspring of the heterozygous Light Brahma male first used in crosses with buffs. The amount of black in the hackles of these birds appeared to be somewhat greater than in the offspring of the Light Brahma cross, but it was not sufficient to serve as a distinguishing mark. White Wyandottes, therefore, may carry a gene for the restriction of buff which is probably the same as the gene found in Light Brahmas and Columbian Wyandottes.[5] It is not demonstrable, of course, except in crosses of White Wyandottes with colored fowls which supply the dominant gene *C* for the development of pigment.

In addition to these three instances of the occurrence of a gene for restriction of buff there are numerous other cases in the literature in which the difference between buff (or red) and white in certain parts of the plumage is apparently due to the same gene or one with similar effects. Davenport (1912) found a sex-linked difference between Dark Brahmas and Brown Leghorns, the gene "W" inhibiting the appearance of buff or red in the hackles and saddles of Dark Brahmas. Jones (1914) was probably dealing with a similar sex-linked gene in his crosses between Silver and Golden Campines, and Hagedoorn's (1914) evidence indicates that the same or a similar sex-linked gene differentiates Silver and Golden Assendelvers. Punnett (1919) distinguishes a sex-linked gene "S," which in crosses of Silver and Golden Campines inhibited the development of buff or gold in the plumage, leaving certain portions of the feather "silver" or white. Most recently evidence presented by Haldane (1921) indicates that black and white barring such as characterizes the Barred Plymouth Rock variety is differentiated from black and buff (or red or gold) barring by the same gene "S" for the inhibition of buff. This sex-linked gene "S," Haldane found to be linked, as was to be expected, with the sex-linked gene "B" (barring).

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[5] Professor W. A. Lippincott has called my attention to this statement in Robinson (1921), p. 42: "The pattern (*i.e.*, Columbian) was also produced by crossing the Rhode Island Red (which has really the same pattern with the black—on a red ground—reduced to a minimum) with a White Wyandotte."

In each of these cases a dominant sex-linked gene was found which restricted or inhibited the development of buff (or red or gold) in certain parts of the plumage. Although in the absence of data on crosses between the varieties mentioned it is impossible to assert that the restriction of buff in the silver or white-patterned varieties is in each case due to the same gene, the presumptive evidence in favor of such a view is strong. It appears probable that Columbian and buff varieties of several breeds (Leghorns, Plymouth Rocks, Wyandottes, etc.) are differentiated by the presence in the Columbians of a gene for the inhibition or restriction of buff pigment; and in view of the history of the various color varieties that this gene has been introduced into and now differentiates Golden from Silver-laced Wyandottes, Golden from Silver Spangled Hamburgs, gold pencilled (or partridge) varieties from silver-pencilled ones and other golden varieties from silver varieties which differ only in the distinction between buff and white in the plumage.

Data on the results of crosses involving these color varieties are urgently needed, and the generalization offered above is put forward as a temporary simplification in lieu of but as an aid to more extensive research.

THE BLACK COMPONENT OF THE COLUMBIAN PATTERN

When the experiments with buff and Columbian fowls were begun it was supposed that at least two alternative characters distinguished these varieties; viz., ground color (white as opposed to buff) and pattern (black in hackles, wing, and tail as opposed to self coloration). The results of these experiments, a reexamination of the parent types and a cursory review of poultry literature indicate the error of this assumption.

1. *Experimental.*—The first generation of the cross Columbian × Buff consisted of birds intermediate between the parental types in the amount of black pigment present. If four arbitrary grades (1–2–3–4) in the reduction of the amount of black in hackles, wing and tail are made between typical Columbian and entire absence of black (white or buff self) then the first generation is found to consist of the following grades.

Columbian	—1	—2	—3	—4	Self
0	8	10	2	0	0

If the buff parents are classified as self then the hybrids resemble the Columbian parent more closely. But a careful examination of all the buff females used revealed the presence in each of them of a small amount of black pigment usually as broken patches or fine stippling in the tail and primary feathers, and occasional traces in the hackles.[6] The buffs, therefore, can not be regarded as selfs and most of those used in these experiments were assignable to grade–4. The amount of black in the F_1 fowls is only slightly above the mid point between Columbian and grade–4.

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[6] It is the experience of farmers and poultrymen, as evidenced in poultry literature, that buff fowls with no admixture of black pigment have been rare. Black in wings and tail is being rigidly selected against and is being gradually reduced in modern breeds.

An F_2 generation has not yet been raised from the cross of typical Columbian × Buff, but some data are available on the F_2 generation from the cross of the heterozygous Light Brahma which was first used in crosses with buff. This male was lighter than typical Columbian, about grade–1. His offspring were not graded but had slightly less black than the offspring of the typical Columbian male, averaging about grade–3. The amount of black was similar in the Columbian and buff progeny. When these F_1 buffs were bred *inter-se* the grades of the F_2 adult fowls were as follows:

Columbian	—1	—2	—3	—4	Self
0	7	13	10	1	0

The variation in amount of black pigment was practically continuous, except that the Columbian parental type was not recovered. No buffs were obtained which were entirely free from black in tails or wings.

The F_1 Columbians were backcrossed with a pure Buff Rock male which showed only faint traces of black stippling (mealiness) in the tail. The progeny of this cross were of the following grades:

Whites (Columbians) and buffs combined:

Columbian	—1	—2	—3	—4	Self
0	2	3	9	13	4

The amount of black in these fowls was obviously much less than in the F_2 generation although the same grades were represented. In four fowls (three buffs and one white) no trace of black pigment could be detected.

It is obvious from these facts that as regards the black component of the Columbian pattern, the Light Brahmas and the buffs used differ only in amount. A blend occurs in the first generation followed by segregation in the second and backcross generation. It is probable, therefore, that the two types crossed differ from each other by multiple factors affecting the amount of black pigment produced. The number of these factors can not be estimated because of the small numbers of animals involved and because a second generation has been bred only from an original cross in which the Columbian parent did not have the amount of black normal to that variety. Failure to recover the typical Columbian pattern in later generations is probably due to the last named circumstance rather than the absence of segregation.

The two varieties probably do not differ by any single factor determining the presence or absence of black pigment, but only in the degree to which black is produced, the degree probably being governed by accessory or modifying factors. This fact attaches especial interest to the appearance of several birds in the backcross generation which show no trace of black pigment. Do these represent loss of a factor determining the ability to develop any black pigment at all or are they segregates in which factors limiting the exercise of the black-producing function are at a maximum? Since they are few in number and since variation in the amount of black grades imperceptibly into the self condition I am inclined to the latter view. If this is true it should be possible to reduce the amount of black in Columbian fowls by rigid selection against it to such a point that birds might be produced which were phenotypically white, but which as regards restriction of buff would breed like Columbians.[7] Such a character would be in effect a sex-linked self white and the absence of a sex-linked white in the many breeds investigated points to the probability that none has been produced in this way.

Much of the interest in the case presented here inheres in the apparent simplicity of the results. The crossing of Light Brahmas and Buff Orpingtons or Buff Plymouth Rocks produces in the first, second and backcross generations only two easily distinguishable types, white (Columbian) fowls and buffs—in which to be sure there is some variation in the amount of black pigment present in certain parts of the body, but apparently no epistatic pattern factors are introduced from either side of the cross to obscure the visible segregation of the main factors. Restriction of buff as found in Columbian fowls is, therefore, a valuable sex-linked gene for use in measuring linkage or in other Mendelian experiments with poultry while buff appears to be the best color variety to be used in studying the inheritance of unknown plumage characters. The Brown Leghorn or game type plumage pattern, although it resembles the supposed wild type form, is in the writer's opinion less valuable than buff because of the often evidenced[8] presence in the genetic constitution of the Brown Leghorn of epistatic pattern factors for extension of black pigment, stippling, etc.

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[7] One such bird has appeared in the course of these experiments; see p. 244.

The general results of the experiments reported have been to confirm and extend the previously known facts regarding the inheritance of the Columbian variation. The genetic relationships of this pattern and the buff coloration also throw some interesting light on the evolution of these two color varieties. They differ, it has been shown, only in one main gene which determines the production or restriction of buff in the plumage. Both are able to develop black pigment in certain parts of the plumage, while they differ quantitatively in the degree to which black may be produced. The former single factor difference probably arose as a single mutation, while the latter and less important difference is one which could be brought about by selection of small variations which had already arisen in a common parental stock.

The variation which produced the chief difference between these two color varieties, *i.e.*, the restriction of buff, undoubtedly took place at least 75 years ago and probably in China, although there is no evidence that the same variation has not occurred several times. The first known Columbian breed was probably the Gray Shanghae, from which the Light Brahmas were derived. These fowls were imported into the United States from China in the decade before 1850[9] and into England shortly afterward. At about the same period and often in the same shipments were imported certain buff birds which eventually became the foundation stock of the Buff Cochin breed from which practically all buff varieties of the present day received their color. These two varieties were practically identical in characters other than plumage color[10] and in the matter of plumage the chief difference was the difference in body feathers, being white more or less stippled with gray in the Shanghaes and buff similarly stippled with gray (mealiness) in the Buff Cochins. In China, observers have regarded the buff as the older color variety while the gray was noted as separate about 1840.[11] The Chinese apparently paid little attention to color in breeding their fowls and the variation from buff to white (or the reverse) in the plumage may have occurred many years or even centuries previous to this date.

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[8] Sturtevant, A. H. (1912); Lefevre, G. (1916).

The further differences between Columbian and Buff breeds have taken place since their introduction from the Orient, chiefly under the selective breeding of English and American poultrymen. The buffs were at first characterized by a great deal of variation in the shade of the principal color—ranging from lemon to red; while the wings, and tails, and tips or margins of the hackles varied from solid black through stippling and blotching to an absence of black in any one of these parts.[12] All subsequent selection has been against the black[13] and the American Standard of Perfection now specifies "buff in all parts of the plumage." In the Shanghaes or Light Brahmas on the other hand the object of the breeder has been to preserve the black in the hackles, wings and tails and to heighten the contrast with the white body by selecting against grayness or mealiness in the body feathers. Two principal processes were apparently involved in the production of buff and Columbian varieties; a discontinuous change or mutation producing the chief difference, and the accumulation by selection of minor factors producing the minor changes. It is impossible to say whether the buff and Columbian varieties which exist at the present time in the principal breeds were derived from these original types by crossing or whether the principal mutation and the minor changes and selection have recurred in the different breeds. The probabilities are in favor of the first alternative.

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[9] Weir, Johnson and Brown, "The Poultry Book," N. Y., 1912, p. 528.

[10] Tegetmeier, W. B., *loc. cit.*, p. 63.

[11] Weir, Johnson and Brown, *loc. cit.*, p. 528.

[12] Weir, Johnson and Brown, *loc. cit.*, p. 527; p. 630, p. 540. Tegetmeier, *loc. cit.*, pp. 40–41.

[13] With the exception of the selection for black in hackles, wing and tail which was employed in developing the Buff Brahma variety.

Summary

1. The Columbian plumage coloration in domestic fowls is distinguished from buff coloration by the presence of a gene *S* which determines the restriction or inhibition of buff pigments from the feathers. This gene is sex-linked, and dominant over its allelomorph *s*, which permits the development of buff pigment.

2. Fowls with the Columbian coloration do not differ from buff fowls in any single gene governing the development of black pigment. Multiple genes appear to determine the difference in the amount of black pigment developed.

3. Columbian and buff fowls are genetically alike in plumage pattern, that is, in the ability to develop black pigment in the feathers of certain areas (hackle, wing and tail feathers).

4. The buff coloration appears to have diverged from the Columbian coloration, or the reverse, by a single gene mutation affecting the development or inhibition of buff pigment; and by the accumulation through artificial selection of multiple genes for the development of black pigment in the Columbian varieties of fowls, and by the reverse selection in most buff varieties.

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